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Simultaneous adaptation to non-collinear retinal motion and smooth pursuit eye movement

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ABSTRACT

Simultaneously adapting to retinal motion and non-collinear pursuit eye movement produces a motion aftereffect (MAE) that moves in a different direction to either of the individual adapting motions. Mack, Hill and Kahn (1989, *Perception*, 18, 649–655) suggested that the MAE was determined by the perceived motion experienced during adaptation. We tested the *perceived-motion hypothesis* by having observers report perceived direction during simultaneous adaptation. For both central and peripheral retinal motion adaptation, perceived direction did not predict the direction of subsequent MAE. To explain the findings we propose that the MAE is based on the vector sum of two components, one corresponding to a *retinal* MAE opposite to the adapting retinal motion and the other corresponding to an *extra-retina MAE* opposite to the eye movement. A vector model of this *component hypothesis* showed that the MAE directions reported in our experiments were the result of an extra-retinal component that was substantially larger in magnitude than the retinal component when the adapting retinal motion was positioned centrally. However, when retinal adaptation was peripheral, the model suggested the magnitude of the components should be about the same. These predictions were tested in a final experiment that used a magnitude estimation technique. Contrary to the predictions, the results showed no interaction between type of adaptation (retinal or pursuit) and the location of adapting retinal motion. Possible reasons for the failure of component hypothesis to fully explain the data are discussed.

1. Introduction

After a period of watching unidirectional motion, a stationary test pattern will appear to move in the opposite direction (the motion aftereffect – MAE). When a stationary fixation point is provided during the adaptation period, the MAE is presumably a consequence of adapting to retinal motion. When the fixation point is removed, the observer is likely to follow the adapting stimulus with a pursuit eye movement. Adaptation now combines signals related to eye movement and to retinal motion, both of which can independently give rise to MAE (Chaudhuri, 1990, 1991; Freeman & Sumnall, 2005; Freeman, Sumnall, & Snowden, 2003).

Moving the eye during adaptation produces two types of retinal motion. Retinal slip occurs when the eye does not track the adapting stimulus accurately. However, the slip produced during pursuit adaptation is often too small and variable to account for any subsequent MAE (Chaudhuri, 1991; Freeman et al., 2003) and is sometimes in the wrong direction (Morgan, Ward, & Brusell, 1976). The second, more influential type of retinal motion occurs when other objects are visible and move differently from the main pursuit stimulus. We refer to this type of retinal motion as *object-dependent*. A number of studies have shown that adapting to object-dependent retinal motion can induce MAE in a central static test (Mack, Hill, & Kahn, 1989; Mack et al., 1987; Morgan et al., 1976; Wade, Spillman, & Swanston, 1996). More recent studies have also shown that simultaneously adapting to eye movement and retinal motion produces changes in perceived motion during pursuit (Dash, Dicke, Chakraborty, Haarmeier, & Thier, 2009; Freeman, 2007; Haarmeier, Bunjes, Lindner, Berret, & Thier, 2001; Haarmeier & Thier, 1996).

When object-dependent retinal motion is absent, a compelling MAE is produced by the eye movement alone (Chaudhuri, 1990, 1991; Freeman & Sumnall, 2005; Freeman et al., 2003). Freeman et al. (2003) termed this the *extra-retinal MAE* because the illusory motion depends on motion signals generated by the oculomotor system (Chaudhuri, 1991), both during and after adaptation. There are a number of important properties that differentiate extra-retinal MAE from its better-known retinal counterpart. First, the extra-retinal MAE is not retinotopic (Chaudhuri, 1991), though we do note that adapting to specific patterns of retinal motion, such as expansion, produces a retinal MAE which is also not retinotopic (Price, Greenwood, & Ibbotson, 2004; Snowden & Milne, 1997; von Grunau & Dube, 1992). Second, the extra-retinal MAE displays

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100% interocular transfer (Swanston & Wade, 1992). Third, adapting to repetitive oblique pursuit eye movements gives rise to an MAE that changes direction over time (Freeman & Sumnall, 2005). The change may be the consequence of adapting separate horizontal and vertical eye movement mechanisms that recover at different rates. Fourth, only deliberate, pursuit-like eye movement gives rise to MAE that stores (i.e. is preserved when a relatively long period of darkness is inserted between adaptation and test). In contrast, adapting to reflexive optokinetic nystagmus produces extra-retinal MAE that dissipates over the storage period (Freeman & Sumnall, 2005).

The existence of the extra-retinal MAE makes predicting the consequence of adapting simultaneously to pursuit and object-dependent retinal motion more complicated than has previously been thought. Consider the situation in which repetitive pursuit is made to a small target moving over a stationary stimulus, with no other objects visible. Assuming the subsequent test appears in approximately the same retinal location as the object-dependent retinal motion, then the combination of extra-retinal and retinal MAE could potentially give rise to three possible directions of illusory motion. Note that in this example the object-dependent retinal motion moves at the same speed but in the opposite direction to the pursuit. Thus the two adapting motions give rise to retinal and extra-retinal aftereffects moving in opposite directions. Assuming these components combine, then if they have equal 'strength' no overall MAE would be seen because the two components cancel. On the other hand, if the extra-retinal component is larger than the retinal component, then a static test should appear to move in the opposite direction to the adapting pursuit. Conversely, if the retinal component is larger, the test should now be seen in the same direction as the adapting pursuit.

The above describes what we refer to as the *component hypothesis*. An alternative to this is the *perceived-motion hypothesis*, which holds that the primary drive for adaptation is the perceived motion experienced during adaptation rather than post-adaptation changes to earlier sensory processes. The perceived-motion hypothesis is based on the idea that the visual system needs to compensate for the retinal motion generated by self-motion, allowing the observer to determine how objects are moving with respect to the ego (Champion & Freeman, 2010; Freeman, 2001; Freeman & Banks, 1998; Freeman, Champion, Sumnall, & Snowden, 2009; Freeman, Champion, & Warren, 2010; Freeman & Fowler, 2000; Haarmeier & Thier, 1996; Haarmeier et al., 2001; Krukowski, Pirog, Beutter, Brooks, & Stone, 2003; Naji & Freeman, 2004; Nefs & Harris, 2007; Perrone & Krauzlis, 2008; Rushton & Warren, 2006; Souman, Hooge, & Wertheim, 2005b; Souman, Hooge, & Wertheim, 2006; Sumnall, Freeman, & Snowden, 2001; Turano & Massof, 2001; Wallach, 1987; Warren & Rushton, 2009; Wertheim, 1987, 1994). This type of hypothesis was favoured by Mack et al. (1989), who studied the perceived direction of MAE following adaptation to vertical pursuit over a stimulus moving horizontally on the screen. In their study the subsequent MAE moved horizontally, suggesting that the MAE was opposite to the perceived motion of the adapting stimulus (as opposed to the oblique object-dependent retinal motion that their vertical pursuit produced). However, they did not measure the perceived motion during adaptation, a point that is central to the current experiments (see below). Moreover, they did not consider how the extra-retinal MAE might influence their results, in part because Chaudhuri's pioneering finding had yet to be published. Thus they only considered one of the two possible component aftereffects that could be elicited by their adaptation sequence, namely that related to object-dependent retinal motion.

Mack et al's results contrast with an earlier report by Anstis and Gregory (1965), who found that only the direction of object-dependent retinal motion was able to predict the perceived direction of the MAE following adaptation to eye movement. However, the pursuit in Anstis & Gregory's study was extremely slow at 0.75°/s, which probably explains the dominance of retinal motion. Further support for the perceived-motion hypothesis comes from motion adaptation during self-motion. Combining retinal expansion and forward self-motion produces MAE that is considerably reduced when compared to 'no self-motion' conditions (Harris, Morgan, & Still, 1981; Wallach & Flaherty, 1975). Assuming the displays in these studies simulated an earth-stationary scene as observers were either pushed to and fro on a moving trolley (Harris et al., 1981) or rocked back and forth (Wallach & Flaherty, 1975), the reduced MAE could be explained in terms of a reduction in perceived motion in the self-motion conditions. Note that these results could also be explained by the component hypothesis, assuming that an analogous extra-retinal MAE can be generated by head movement.

The paradigm developed here makes use of the fact that perceived motion is biased towards the direction of the object-dependent retinal motion when retinal motion and pursuit are non-collinear (Becklen, Wallach, & Nitzberg, 1984; Festinger, Sedgwick, & Holtzman, 1976; Souman, Hooge, & Wertheim, 2005a; Souman et al., 2005b, 2006; Swanston & Wade, 1988). In our experiments pursuit adaptation was combined with oblique motion on the screen. For accurate eye movement, this produces horizontal retinal motion as shown in Fig. 1 (note that Mack et al. (1989) combined vertical pursuit with *oblique* retinal motion). According to the perceived-motion hypothesis, the subsequent MAE should therefore be biased towards horizontal, as shown by the broken grey arrow. Predictions for the component hypothesis depend on the magnitude of the components produced by adaptation. Upward pursuit and leftward retinal motion produce rightward retinal MAE and downward extra-retinal MAE, respectively (broken blue and red arrows). So, as Fig. 1 shows, if the magnitudes of the components are the same, the MAE should move obliquely according to the component hypothesis (broken black arrow).

In the current study we therefore had observers adapt to pursuit and retinal motion moving in orthogonal directions at the

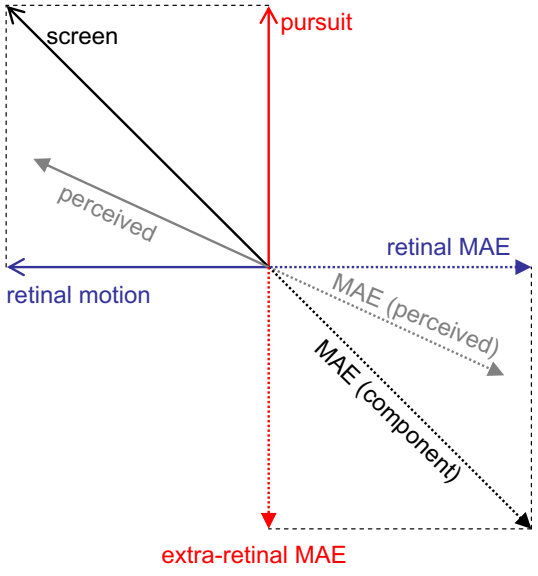

Fig. 1. Example predictions for the perceived-direction and component hypotheses. Adaptation directions are shown with solid arrows while perceived-adaptation directions and putative MAEs are shown with broken arrows. The perceived direction during adaptation (solid grey arrow) is deliberately rotated towards the adapting retinal motion (solid blue arrow) on the basis of previous findings (see text for details). The perceived-direction hypothesis predicts an MAE in a direction that is opposite to this (broken grey arrow). The component hypothesis predicts an MAE (broken black arrow) that is the vector sum of retinal an extra-retinal MAE (broken blue and red arrows). In the schematic these are assumed to be of equal magnitude.

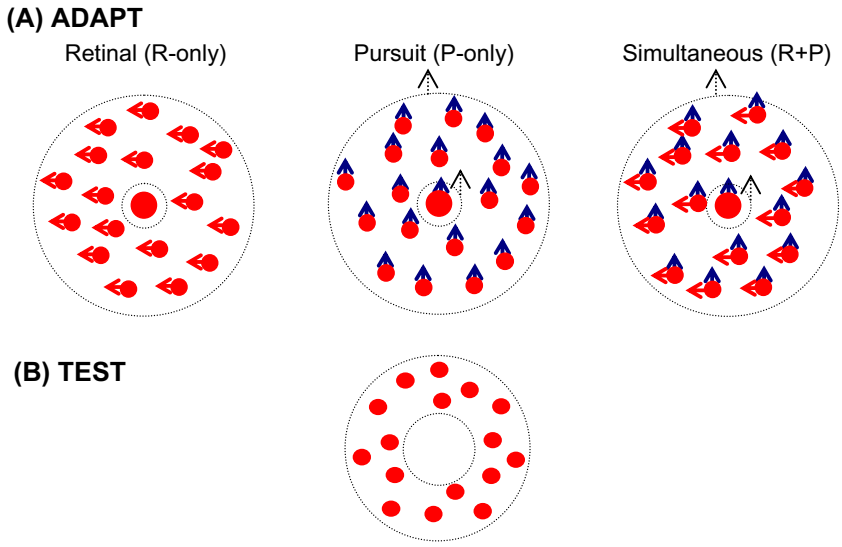

Fig. 2. Illustration of the adaptation and test stimuli used in the experiments. (A) The three stimuli at the top depict the retinal only, pursuit-only and retinal-plus pursuit adaptation conditions (labelled R-only, P-only and R + P). Assuming accurate fixation or pursuit, the red arrows show the velocity of the adapting retinal motion and the blue arrows the adapting pursuit (speed was 4°/s in both cases). The R + P dot pattern therefore moved obliquely on the screen, up and to the left. (B) The smaller annulus stimulus depicts the static test pattern (note that in all cases the red dots were actually presented on a black background in a dark room).

same speed. During adaptation, observers made concurrent judgements about the direction of the non-pursued adaptation pattern. These were then compared to the velocity of the subsequent MAE. In the first two experiments we measured the direction of MAE only. Experiment 1 placed the pursuit target and adapting retinal motion centrally, whilst Experiment 2 moved the retinal motion stimulus into the periphery. We also included separate pursuit-only (P-only) and retinal-only (R-only) adaptation conditions, which allowed us to check whether the essential ingredients for the component hypothesis were in place. In anticipation, the results of the first two experiments did not support the perceived-motion hypothesis. But in order for the component hypothesis too fully explain the results, a linear vector model showed that the magnitude of the extra-retinal MAE had to be considerably greater than the retinal MAE for central adaptation (Experiment 1), and about the same for peripheral adaptation (Experiment 2). This prediction was tested in the final experiment, which measured the speed of the MAE produced by the P-only and R-only conditions, using a magnitude estimation technique.

2. Experiment 1: Central retinal adaptation

2.1. Method

2.1.1. Stimuli

Stimuli were generated on a PC using a Radeon 9800 Pro graphics card and presented on a Viewsonic P225F 19 inch monitor. The visual stimuli were generated using OpenGL. The screen was viewed binocularly through a red gel absorptive filter to reduce screen glow and dot trails. Both adaptation and test were presented on a black background in a completely darkened room. A chin rest and forehead bar maintained a stationary head at a constant viewing distance of 57.3 cm.

There were three conditions: retinal-only adaptation, pursuit-only adaptation and simultaneous adaptation that combined retinal motion and pursuit. We refer to these as R-only, P-only and R + P. The adaptation conditions were achieved using the stimuli illustrated in Fig. 2. Each consisted of a random dot pattern (density of 1 dot/deg) comprising dim red dots (~2.8 cd/m^2, radius 0.1°) and a larger fixation point (radius 0.2°). The random dot pattern was presented within an annulus window (inner radius 0.5°, outer radius 5°). When retinal motion was required in the R-only and R + P conditions (left and right panels of Fig. 2), the random dot pattern moved to the left with respect to the moving window at a speed of 4°/s (red[2] arrows Fig. 2). When pursuit was required in the P-only and R + P conditions (middle and right panels), the fixation point, annulus window and dots all moved vertically upwards at 4°/s (blue arrows in Fig. 2). On the screen, therefore, the dots moved obliquely up and to the left in the R + P condition, so assuming accurate pursuit, the retinal motion was identical to the R-only condition. The position of the adapt stimuli was a sawtooth function of time, consisting of a 1 s sweep of adapting motion followed by an abrupt return (inset to Fig. 2). A new random dot pattern was generated following each sweep.

Following 50 s adaptation, a central fixation point was displayed for 1 s to encourage stationary fixation during test. The fixation point then disappeared and was replaced by a stationary annulus test pattern for 5 s (bottom right panel of Fig. 2). Participants were instructed to keep their eyes as still as possible during this period and fixate the blank centre of the annulus. The dimensions of the test annulus (inner radius 1°, outer radius 4°) were made smaller than the adaptation annulus so that the test pattern covered an area 'inside' the previously-seen adaptation pattern. The reduced size helped ensure that the entire test area had been strongly adapted by retinal motion, even when pursuit or fixation had been somewhat inaccurate. In addition, the reduction mitigated possible edge effects, such as the 'peculiar MAE' confined to the edge of a test grating reported by (Murakami & Shimojo, 1995), which they attributed to small fixation errors during adaptation.

2.1.2. Procedure

During adaptation and test, perceived direction was recorded using a purpose-built pointing device attached to a table in front of the observer. The pointing device consisted of an arm mounted on a box that could be rotated horizontally to indicate perceived

[2] For interpretation of colour in Figs. 1–4 and 10, the reader is referred to the web version of this article.

direction via a potentiometer. Physical stoppers could be placed in several positions to limit the arc of rotation as required. The plane of rotation was approximately at right-angles to the screen. The potentiometer was sampled using a 16-bit data acquisition card (NIDAQ BNC-2110).

The pointing device required observers to map perceived direction seen in one plane onto felt direction in another. This could potentially introduce unwanted biases into the main experiments. For this reason, the mapping was calibrated prior to data collection by having each observer make settings to 15 centrally-presented dot pattern motions moving physical at 0.5°/s. The 15 calibration conditions ran from −112.5° to 202.5° in 22.5° steps; observers made two settings per direction, yielding a total of 30 calibration settings. The calibration stimuli had the same dimensions as the test stimulus used in the main experiment, except that the central static fixation point remained visible throughout each calibration run. The calibration stimuli were displayed for 3 s. A 3rd-order polynomial was then fit to the calibration data to quantify the mapping separately for each observer. The fitted polynomial was then used to convert potentiometer voltages obtained in the main experiment into perceived directions measured in degrees, thereby removing any potential biases. We note in passing that asking observers to map measurements and percepts between different planes, or indeed perform some more complex mental rotation, are techniques that are not without precedence (e.g. motion-in-depth: Harris and Dean (2003); slant-from-motion: Harris, Freeman, and Hughes (1992)). Indeed, Harris and Dean (2003) found their results did not depend on which of the four techniques they used, some of which required mapping between two planes and others that required mental rotation.

In the main experiment, four replications of the three adaptation conditions were carried out. The 12 trials were presented in random order. Each started with 50 s of light adaptation to a bright homogeneous screen, which served to both keep the observer somewhat light-adapted and also allow dissipation of any MAE between trials. Adaptation to motion followed for a further 50 s, during which participants continuously indicated the direction of the adapting motion using the pointing device. The test then appeared for 5 s and observers indicated its perceived direction. During the test phase, observers were allowed to take as long as they needed to set the pointing device once the test had disappeared. They were also given the option of indicating that they had experienced no MAE by leaving the pointer bar in the leftward starting position (against the physical stopper). Once satisfied with their setting, observers terminated the trial with a mouse click.

2.1.3. MAE analysis

During the adaptation phase, perceived direction was sampled once per motion sweep. The first five samples (i.e. five adaptation sweeps) were removed to account for the initial adjustment of the pointing device from an arbitrary start position. We did not examine the time-course of perceived direction. Hence perceived direction during adaptation was defined as the mean across the remaining 45 samples. During the 5 s test period, only the final setting was used to define the direction of the MAE. If the observer did not experience an MAE, the trial was discarded from the analysis. Data were then averaged over the remaining trials for each observer.

Two observers made one anomalous direction setting during the adaptation phase, reporting that the perceived direction of the moving random pattern was in fact opposite to the actual adapting motion. We attributed these to mistakes and deleted the two trials from the analysis.

2.1.4. Eye movement recording and analysis

Eye movements were recorded monocularly for all participants in all trials using an ASL series 5000 head-mounted eye tracker sampling at 60 Hz. The eye tracker was calibrated using a 3 by 3 array of points prior to data collection. No drift correct was implemented – but note that we were interested in eye velocity, so any positional shifts would be cancelled out by subsequent differentiation in the analysis.

The eye movements were analysed in MatLab using a combination of custom-built and ASL eye tracker software. The eye movement data were first smoothed with a Gaussian filter (SD = 16 Hz) and velocity and acceleration profiles calculated for both X and Y channels by differentiating each with respect to time. Saccades were then detected and excluded from further analysis as follows. The centre of a saccade was defined as a zero-crossing in the acceleration profile that also coincided with a velocity that exceeded a threshold of 35°/s above the speed of the pursuit target. When a saccade was detected in either X or Y channels, eye-tracker samples ±83 ms either side were removed from both X and Y velocity profiles. Eye blinks were also removed. Fig. 3 shows an example position profile from one observer, using the eye movements recorded during an R + P trial. The bottom trace shows the expected Y component, which ideally should resemble a sawtooth wave. The top trace shows the X component and indicates that this observer was unable to perfectly track the stimulus vertically – the velocity profile therefore contains a low amplitude sawtooth wave. The red and black portions in the position profiles show the result of the saccade analysis, with red corresponding to sections deemed saccadic.

Eye velocity was summarised using the 'non-saccadic' portions of each trace. We report both the X and Y components in the results section and also the mean (across samples) of eye speed $(X^2 + Y^2)^{0.5}$ and direction $\arctan(Y/X)$ for each adaptation run. Mean eye speed was converted into pursuit gain by dividing by the target speed. Trials in which mean eye speed deviated by more than two standard deviations from the overall mean per observer were removed.

2.1.5. Participants

Twenty-five undergraduate psychology students at Cardiff University, with normal or corrected to normal vision, took part in Experiment 1 for course credit. Four participants did not experience an MAE during the experiment and were excluded. All participants provided informed written consent and were fully debriefed after completing the experiment.

2.2. Results

2.2.1. Perceived direction

Fig. 4 plots the mean perceived direction during the three adaptation conditions (solid arrows) and during MAE (dotted arrows), averaged across observers. Individual data are shown as points. Different coloured arrows correspond to the results for different adaptation conditions, with the solid arrows in the top-left quadrant corresponding to the settings made in the adaptation phase, and the dotted arrows in the bottom-right quadrant corresponding to the test phase. The directions reported during R + P adaptation (solid black arrow) agree with previous findings discussed above, showing that perceived direction during non-collinear pursuit tends toward the object-dependent retinal motion.

The critical test of the perceived-motion hypothesis is how the directions seen during adaptation and test relate to each other in the R + P condition (as discussed below, it is critical because the perceived motion during adaptation is different from the physical motion of the adaptation stimuli). According to this hypothesis, the MAE should be opposite to the direction perceived during adaptation. The mean of this prediction is shown in grey in the

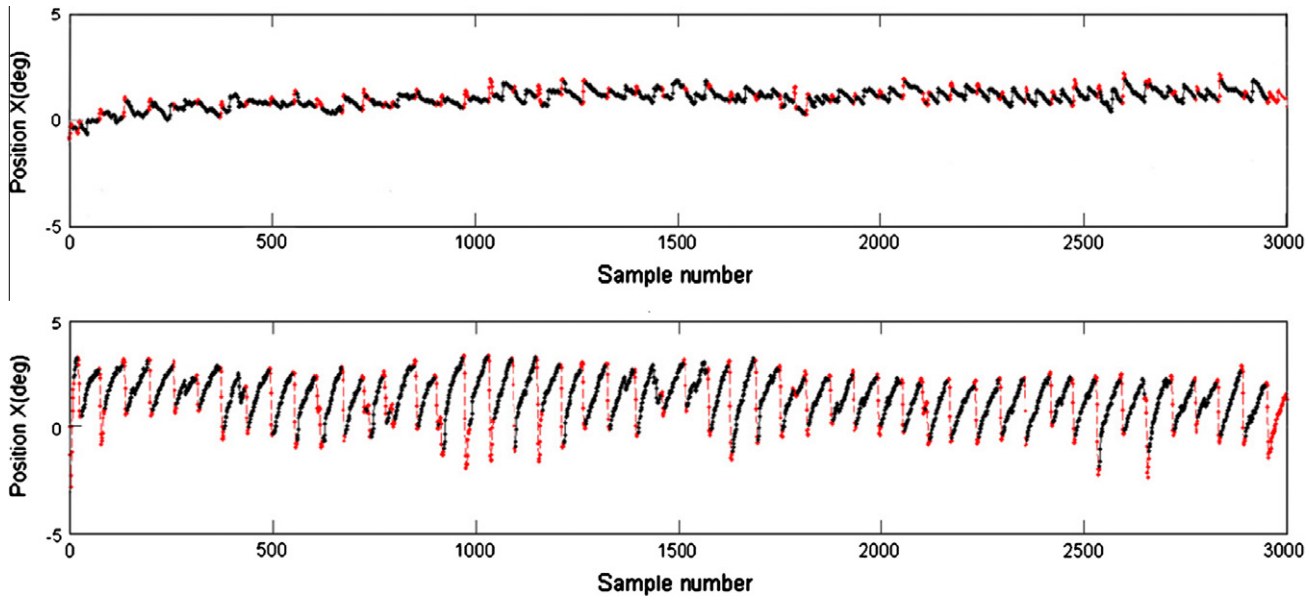

Fig. 3. Eye movement traces in the *X* and *Y* channels for one sample adaptation period (R + P condition). Red sections show parts of the traces deemed 'saccadic' and removed from the analysis.

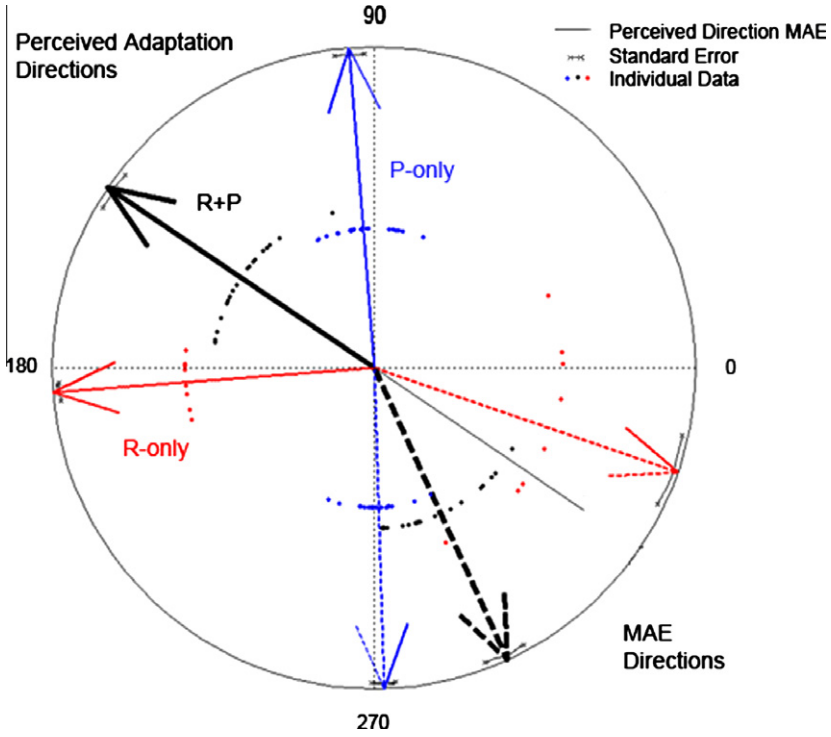

Fig. 4. Mean perceived directions during adaptation and test for the R-only condition (red), P-only condition (blue) and R + P condition (black). The solid arrows represent the perceived direction during adaptation and the dotted arrows showing the direction of the related MAE. The grey lines at the end of each arrow indicate ±1 standard error, with the points showing individual data.

lower-right quadrant of Fig. 5. To test the perceived-direction hypothesis, we added 180° to each observer's perceived direction during adaptation and compared the transformed data to the MAE directions, using a within-subjects *t*-test. The results showed that MAE direction deviates significantly from the prediction ($t(19) = 7.1$, $p < 0.001$; Hedge's $g = 1.97$; note that df $\neq 20$ because one observer failed to report an MAE in this condition). On this basis the data do not support the perceived-motion hypothesis. Whether they support the component hypothesis is discussed later.

Fig. 4 also shows the results for the R-only and P-only conditions. Each produced an MAE, with the latter confirming previous reports that adaptation to pursuit alone gives rise to illusory motion (Chaudhuri, 1991a, 1991b; Freeman & Sumnall, 2005). During adaptation, perceived direction was close to the physical direction of retinal motion or pursuit. The resulting direction of the MAEs cannot therefore differentiate between the two hypotheses – the component hypothesis predicts a direction opposite to the physical retinal motion or pursuit and the prediction for the perceived-motion hypothesis is very close to this. Of course, this assumes that

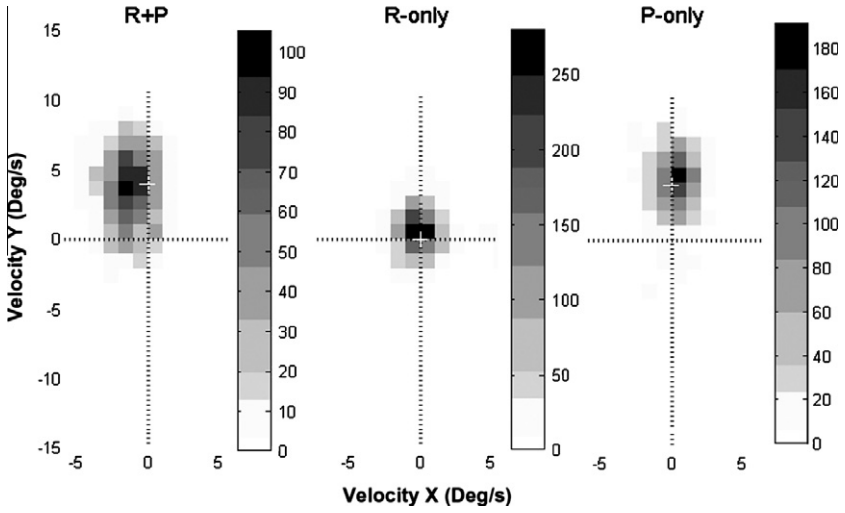

Fig. 5. Example eye movements from one observer during one trial of adaptation for each of the three conditions. The data are shown as 2D velocity histograms. The 1 deg^2 bins are shaded darker as the number of (five sample moving average) eye velocities falling within them increases. The white '+' sign indicates the velocity of the fixation point.

fixation or pursuit were accurate during adaptation in the R-only and P-only conditions, which the eye-movement results reported below show to be approximately the case.

The mean direction of the MAE reported in the P-only condition is as expected. However, the mean direction reported in the R-only condition is rotated clockwise from the predictions of either hypothesis (dotted red line in Fig. 4). We note that the failure to see any MAE in this condition was much higher (76% failure rate in the R-only condition, compared to 33% and 22% in the P-only and R + P conditions, respectively). Hence drawing any conclusions on the basis of such a poorly sampled condition is difficult, especially given that the data are also quite variable. Nevertheless, a *t*-test that compared the perceived-motion prediction in the R-only condition against the MAE direction was not significant ($t(7) = -2.17$, $p > 0.05$, Hedge's $g = 1.02$; the same was also true for the P-only condition: $t(19) = 0.74$, $p > 0.05$, Hedge's $g = 0.22$). To reiterate, given that the component predictions lie close to this, the data in the R-only and P-only conditions could therefore be predicted by either hypothesis.

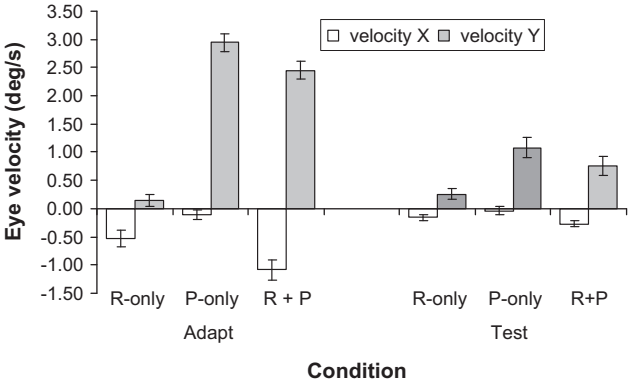

Fig. 6. Mean eye-movement velocities recorded during adaptation (left bars) and test (right bars) for the three separate conditions. The eye movements are reported separately for the *X* component (white bars) and *Y* component (grey bars). Note that adaptation trials in which observers subsequently failed to experience an MAE have been excluded. Error bars correspond to ±1 standard error.

2.2.2. Eye movements

Fig. 5 shows a summary of the eye movements for one observer in the three adaptation conditions. The 2D histograms were constructed from the *X* and *Y* velocity components and are plotted in this Cartesian space. The pursuit target is shown as a white cross. For this observer, fixation in the R-only condition was reasonably accurate, as was pursuit in the P-only condition. However, the introduction of orthogonal retinal motion in the R + P condition caused the eye movements to deviate away from the vertical pursuit target somewhat, in the direction of the object-dependent retinal motion.

These trends were similar across all observers. Fig. 6 plots the mean eye-velocity components for the adaptation phase (left bars) and test phase (right bars). In the R-only condition, observers were able to hold their eyes reasonably still. In the P-only condition, eye movements were vertical (the components yielded a direction of 92°) but at a slower speed than the pursuit target (mean pursuit gain was 0.74). In the R + P only condition, the eyes deviated away from vertical due to the influence of the surrounding retinal motion (mean direction = 117°, gain = 0.68). The inaccuracy in eye movement in the presence of a moving background is in keeping with previous reports (Suehiro et al., 1999; Masson, Proteau, & Mestre, 1995; Niemann & Hoffmann, 1997).

The accuracy of fixation during the test phase is shown in the right-hand bars of Fig. 6. It is important for the eye to be as still as possible in this phase because any significant eye movement will cause retinal motion that could potentially be misinterpreted as MAE if the visual system fails to fully compensate for the eye movement (e.g. the Filehne illusion – see Wertheim, 1994). Although the figure indicates small eye movements, as might be expected, visual inspection of the velocity traces suggested that the overall direction of the eye movement was not related to the direction of the MAE reported. This was confirmed in a further analysis of the R + P condition. The analysis compared the MAE directions in two groups of trials, segregated using a median split defined by the speed of the *X* component. No significant difference existed for the MAE directions reported between these two groupings ($t(63) = 0.76$, $p = 0.45$).

The results of the eye movement analysis show that pursuit during R + P adaptation was far from perfect. Finding inaccurate eye movements could have important ramifications for the component hypothesis. This predicts that MAE following R + P adaptation is the sum of two vectors corresponding to motion components

that 'move' in directions opposite to the adapting retinal motion and pursuit, respectively. Inaccurate pursuit will change the speed of the adapting motions and therefore the magnitude of the corresponding components. Moreover, even if inaccurate pursuit produced adapting speeds that were the same, this does not necessarily mean the magnitude of the components are similar. This issue is developed in more detail in a later modelling section.

Before examining perceived speed, we first attempted to increase the frequency of MAE reported following R-only adaptation, by moving the adapting dot pattern into the periphery. This manipulation was based on previous research showing that peripheral retinal motion often increases the magnitude of retinal MAE. For instance, the velocity needed to null a peripheral retinal MAE is greater (Wright, 1986) and the effect of a modulating surround on MAE increases with eccentricity (Murakami & Shimojo, 1995). Indeed, an increase in the strength of peripheral MAE was suggested by Morgan et al. (1976) as a possible explanation for the induced MAE they found.

3. Experiment 2: Peripheral retinal motion adaptation

3.1. Method

3.1.1. Stimuli and procedure

We used the same stimuli as Experiment 1 but moved the centre of the adapting retinal dot pattern so that it was positioned 10° to the right of the pursuit target/fixation point. During the calibration and test phases, the random dot patterns were displaced peripherally by the same amount.

3.1.2. Participants

Sixteen students were recruited in the same way as Experiment 1.

3.2. Results

3.2.1. Perceived direction

Peripheral adaptation successfully reduced the failure to report MAE in the R-only condition (48% as opposed to 76% in Experiment 1). However, the failure rates for the other two conditions were 47% (P-only) and 31% (R + P condition), both somewhat higher than Experiment 1. Overall, therefore, the failure rates across the two experiments were roughly the same (44% in Experiment and 42% in Experiment).

Fig. 7 plots the mean perceived directions during adaptation and test. The increase in MAE reports for the R-only condition produced MAE directions closer to horizontal. As in Experiment 1, the predictions based on the perceived directions did not differ significantly from the reported MAE directions in the R-only condition ($t(12) = 2.0$, $p > 0.05$, Hedge's $g = 0.77$) and P-only condition ($t(10) = 0.945$, $p > 0.05$, Hedge's $g = 0.32$). But to reiterate, both hypotheses make virtually the same predictions for these two control conditions and so cannot differentiate between the two models. The crucial test is the R + P condition, where perceived motion during adaptation differs substantially from the physical adapting motions. The reported MAE directions significantly differed from the perceived-motion prediction for this condition, as shown in grey ($t(12) = 2.23$, $p < 0.05$, Hedge's $g = 0.86$). Hence the results provide little support for the perceived-motion hypothesis.

3.2.2. Eye movements

Fig. 8 shows the mean eye movements for the adaptation (left bars) and test phase (right bars) for the three conditions. The results showed that pursuit eye movements were close to vertical for the P-only and R + P conditions, both averaging 96°. Placing the random dot pattern peripherally produced a reduction in eye movement gain for both the P-only condition (gain = 0.63) and the R + P condition (gain = 0.59). Fig. 8B shows that unwanted eye movements in the test phase were also reduced.

3.3. Model of the component hypothesis

The results of Experiments 1 and 2 do not support the perceived-direction hypothesis. Here we construct a linear vector model of the component hypothesis to explore the influence of inaccurate pursuit adaptation and the magnitude of the underlying components on subsequent MAE direction.

Consider a pursuit eye movement (P) to a target (T) moving vertically over oblique screen motion (S), as shown in Fig. 9. The adapting retinal motion (R) is the difference between screen motion and pursuit:

$$\mathrm{R} = \mathrm{S} - \mathrm{P} \tag{1}$$

When the adapting eye movement is accurate, the retinal motion is horizontal (labelled R_i in figure). However, Experiment 1 showed that pursuit (P) moved closer to the direction of S. This produces retinal motion that also moved in a direction closer to S, as shown in the figure. According to the component hypothesis, the resulting MAE is the sum of retinal and extra-retinal components moving in a direction opposite to R and P:

$$\mathrm{M} = -(r\mathrm{R} + e\mathrm{P}) \tag{2}$$

The scaling factors r and e express the relationship between adaptation speed (pursuit or retinal) and the respective magnitude of motion aftereffect components. Substituting (1) into (2) gives:

$$\mathrm{M} = -(r\mathrm{S} + (e - r)\mathrm{P}) \tag{3}$$

According to the component hypothesis, the direction of the MAE is therefore independent of actual pursuit when the scaling factors are identical ($r = e$); moreover, when this is the case, the MAE is predicted to move opposite to the screen motion of the dot pattern (S). Experiment 2 showed that peripheral motion adaptation produced an MAE approximately opposite to the screen motion, suggesting that this condition produces retinal and extra-retinal MAEs of approximately equal magnitude.

The central adaptation used in Experiment 1 is more difficult to interpret because: (1) the perceived direction of the MAE in the R + P condition was not opposite to the screen motion; and (2) pursuit during adaptation was inaccurate. Fig. 10 shows predicted MAE directions for a range of scaling factor differences ($e - r$) and pursuit eye movements. The pursuit vectors used to generate each curve are shown in the inset, including the actual mean pursuit found in Experiment 1 (red vector and curve). All curves pass through a direction of −45° when the difference between scaling factors is 0. This confirms the fact that MAE for identical scaling factors is independent of the actual eye movement and always directed opposite to the screen motion. For eye movements in the hemi-quadrant that includes the values recorded in Experiment 1 (see inset), the MAE is always <−45°. In other words, whenever the MAE has a larger downward component, the magnitude of the extra-retinal component should be larger than the retinal component. We note that $e = 1$ in the simulation. Changing the absolute values of the scaling factors alters the 'slopes' of the curves shown in Fig. 10. However, the gross features described above remain the same.

The results of Experiment 1 therefore predict that extra-retinal MAE should have a greater magnitude than retinal MAE when R-only adaptation is positioned centrally. In contrast, the results of Experiment 2 predict that the magnitude of the two MAEs should be about equal when R-only adaptation is peripheral. These predictions were tested in Experiment 3.

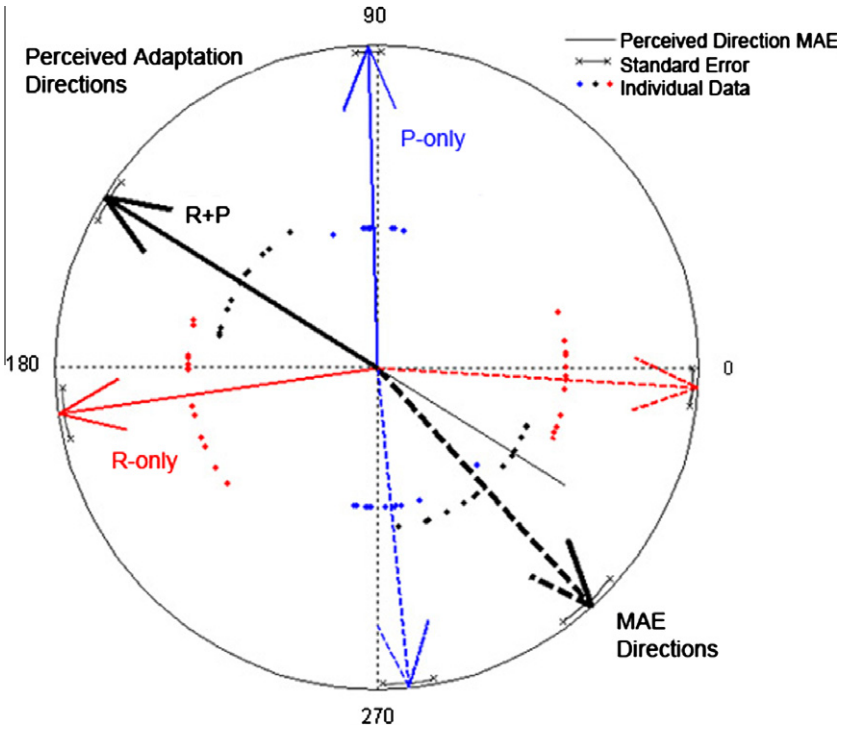

Fig. 7. Mean perceived directions during adaptation and test for Experiment 2.

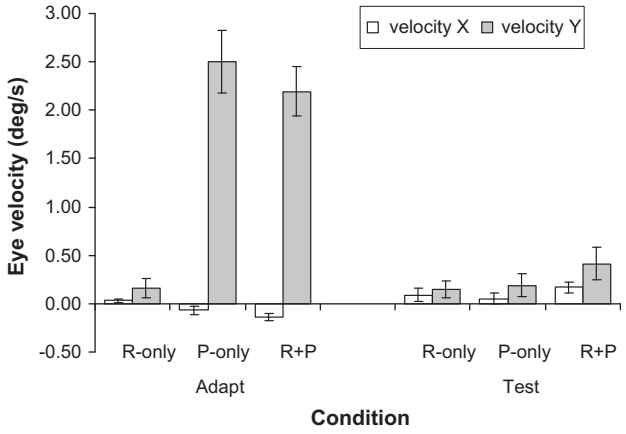

Fig. 8. Mean eye movements in the adaptation (left bars) and test phases (right bars). Error bars correspond to ±1 standard error.

4. Experiment 3: Magnitude of the component MAEs

A typical method used for measuring the magnitude of retinal MAE is a matching procedure in which the perceived speed experienced in adapted and non-adapted retinal areas is compared over a series of trials. The underlying assumption is that particular retinal MAE under test is retinotopic. Unfortunately, extra-retinal MAE is not retinotopic (Chaudhuri, 1991; Freeman et al., 2003). Experiment 3 therefore used a magnitude estimation procedure, where observers indicated the speed of MAE by thinking of the pointing device as a speedometer and setting it accordingly.

4.1. Method

4.1.1. Participants

Sixteen students with normal or corrected to normal eyesight participated. All participants gave informed written consent.

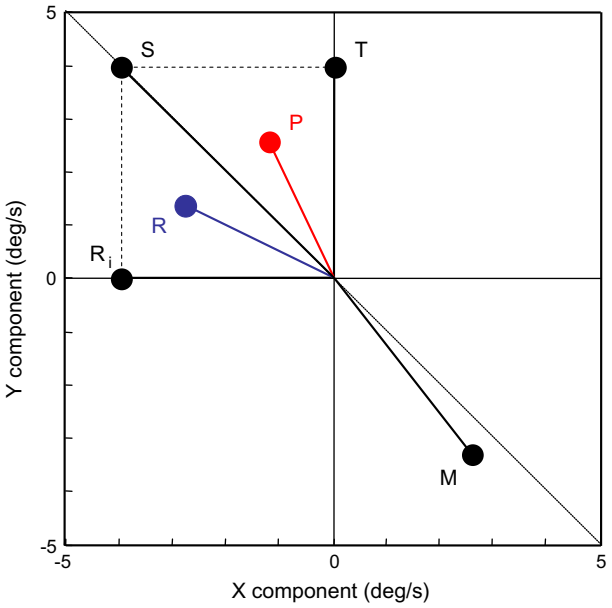

Fig. 9. Model of the component hypothesis. The vectors shown are: pursuit target (T); screen motion (S); retinal motion assuming accurate pursuit (R_i); actual pursuit (P); actual retinal motion (R); motion aftereffect (M), where $M = -(rR + eP) = -(rS + (e - r)P)$ (see text for derivation). In the example show, the scaling factors were set to $e = 1$ and $r = 0.5$.

4.1.2. Stimuli and procedure

The P-only and R-only adaptation conditions of Experiments 1 and 2 were used to yield four conditions: central and peripheral adaptation crossed with type of eye movement (pursuit or fixation). Note that inevitably test pattern location was confounded by the location of the adapting dot pattern. Two replications for all four conditions were presented in random order. Observers indicated the speed of any subsequent MAE by using the unseen

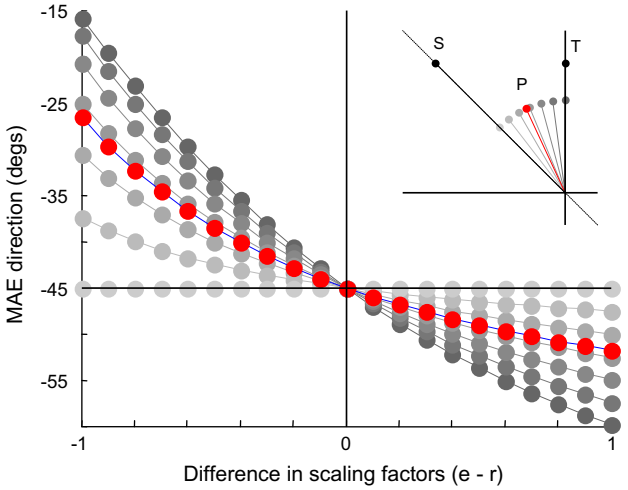

Fig. 10. Direction of MAE as a function of the difference between scaling factors. Each curve corresponds to a different pursuit as defined by the inset. The red curve corresponds to the actual pursuit found in Experiment 1.

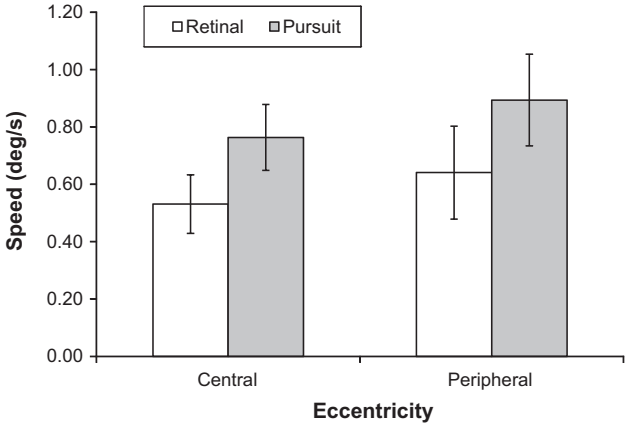

Fig. 11. MAE speed for the four conditions of Experiment 3. Error bars are ±1 standard error.

pointing device as if it was a 'car speedometer'. The pointing device was restricted to an approximately 180° turn, such that fully left indicated 'minimum' speed and fully right indicated 'maximum'. Prior to data collection, a training/calibration phase was run. Observers were first shown examples of stimuli moving at a speed of 4°/s ('maximum' speed) and stationary stimuli ('minimum' speed) and asked to adjust the pointing device accordingly. A number of moving stimuli were then shown, ranging in speed from 0°/s to 4°/s in 0.8°/s steps. The stimuli were presented twice in a random order, both centrally and peripherally. Speedometer settings were averaged and a third order polynomial fitted to produce a calibration curve that mapped perceived speed (defined as the potentiometer voltage) onto physical speed. These were then used to convert the potentiometer settings in the main experiment into perceived speed.

Unlike Experiments 1 and 2, observers did not make any perceived-motion settings during the 50 s adaptation phase.

4.1.3. MAE analysis

Any trials corresponding to an MAE speed of 0 were removed. Only participants with at least one non-zero speed registered in all four conditions were included in subsequent analysis.

4.1.4. Eye movement recording and analysis

Eye movements were recorded using an SR Research Eyelink 2000 eye tracker mounted into the chin rest. The eye movements were sampled at 1000 Hz and analysed in MatLab using custom-developed software similar to that used in Experiments 1 and 2,

4.2. Results

4.2.1. Perceived speed

Fig. 11 shows mean MAE speeds for the four conditions. Central adaptation conditions are shown on the left and peripheral adaptation conditions shown on the right. The data suggest an increase in MAE speed following pursuit, a result confirmed in a two-way ANOVA that showed a main effect of eye movement type ($F(1, 7) = 5.70$, $p \leqslant .05$, $\eta^2 = 0.45$). However, the small increase in MAE speed for peripheral adaptation did not reach significance ($F(1, 7) = 4.32$, $p = 0.076$, $\eta^2 = 0.38$). Importantly, the predicted interaction between location and type of eye movement was not significant ($F(1, 7) = 1.23$, $p = 0.303$, $\eta^2 = 0.15$). The data therefore do not provide unequivocal support for the component hypothesis because the difference in perceived speed was the same for central and peripheral adaptation.

The low frequency of R-only MAE reports in Experiment 1 was not found for the central adaptation condition in Experiment 3, with retinal MAE reported in 69% of trials for central adapt. Extra-retinal MAE was also reported in 69% of trials. For the peripheral adaptation, a retinal MAE was reported in 50% of trials whilst a pursuit MAE was reported in 78% of trials. We can offer little explanation for these differences between Experiments 1 and 3. However, as we argue in the Discussion, these differences are likely to obscure straightforward conclusions about the ability of the component hypothesis to explain the data.

4.2.2. Eye movements

The eye movements were similar to those recorded in the P-only and R-only conditions of Experiments 1 and 2. Fig. 12A summarises performance during adaptation. The mean direction of pursuit was accurate at 90.4° in central condition and 91.8° in the peripheral condition, with gains of 0.69 and 0.7 respectively. During retinal conditions observers held their eyes stationary with a gain of 0.12 for central and 0.11 for peripheral fixation. During the test phases participants held their eyes stationary for all conditions (mean eye velocity <0.06°/s).

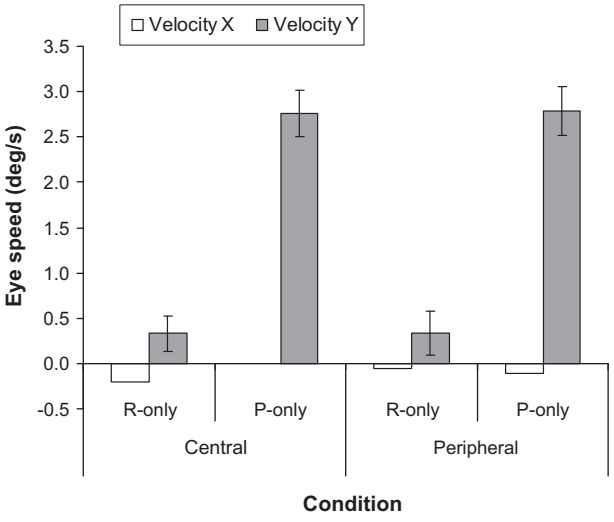

Fig. 12. Mean adaptation phase eye movement velocities in the *X* and *Y* planes for the four conditions in Experiment 3.

5. General discussion

This study investigated the unidirectional MAE that follows adaptation to orthogonal retinal motion and smooth pursuit eye movements. The direction of the MAE reported by our observers was neither opposite to the adapting retinal motion direction nor opposite to the adapting eye movement. Instead the MAE was oblique, appearing to result from some combination of the two adapting motions. This finding is in keeping with the results of Mack et al. (1989), who suggested that the direction of the aftereffect was based on the motion perceived during adaptation. However, they did not measure the perceived direction experienced by their observers, basing their proposal instead on anecdotal reports. To test the perceived-motion hypothesis, we therefore measured perceived direction during adaptation and compared the result to the perceived direction of any MAE subsequently experienced. We found the perceived directions reported during adaptation were similar whether the retinal motion stimulus was placed centrally (Experiment 1) or peripherally (Experiment 2). However, the direction of the MAE following simultaneous adaptation to pursuit and retinal motion was different in both cases and did not move opposite to the perceived direction experienced during adaptation. Our results therefore do not support the perceived-motion hypothesis.

We explored the ability of the alternative component hypothesis to explain the data. This hypothesis is based on the idea that separate retinal and extra-retinal aftereffect components generated by adaptation are combined vectorially to produce the MAE. We constructed a vectorial model to understand how different combinations of adaptation speed (pursuit and retinal) and different magnitudes of component aftereffects would affect MAE direction. The model showed that in order to explain the different MAE directions found during central adaptation (Experiment 1), the magnitude of the retinal component should be substantially smaller than the extra-retinal component. For peripheral adaptation (Experiment 2), however, the model showed that the magnitudes of the two components should be about the same. This prediction was tested in Experiment 3, using a variant of the magnitude estimation technique. The results provide equivocal support for the component hypothesis. Both adaptation locations produced about the same difference in MAE speed, with the speed of extra-retinal MAE always larger.

The ability of the component hypothesis to explain the current data set is therefore open to question. However, we believe that rejection of this hypothesis is premature for two reasons. The first is based on differences in the failure to report MAEs in the central adaptation conditions of Experiments 1 and 3. In Experiment 1, the failure rate in the R-only condition was high whereas in Experiment 3 the failure rate was low. While we can offer no explanation of this finding, the difference in failure rate makes predicting the underlying magnitudes of the retinal and extra-retinal components somewhat difficult. Closer inspection of the individual data in Experiment 1 indicates considerable overlap in the directions seen following P-only adaptation and R + P adaptation. In Experiment 2, however, the overlap is much less. This suggests that the mean MAE direction following the R + P condition of Experiment 1 may have been influenced by a significant minority of observers who had no retinal MAE component when adapting simultaneously to retinal motion and pursuit. In effect, therefore, R + P adaptation for those observers was tantamount to P-only adaptation. Experiment 3 used different observers and did not find such high failure rates. On this basis it is difficult to resolve the differences between the two experiments in terms of the component hypothesis.

The second reason we believe rejection of the component hypothesis is premature concerns the use of magnitude estimation. In order to 'bootstrap' this technique the observers first had to map a range of physical speeds onto a somewhat arbitrary representation of speed defined by the speedometer device. Whether the calibration phase provided enough training, and whether the initial mapping acquired during training remained stable across the course of the experiment, is debatable. It is less easy to level such a criticism when using the device to indicate direction (as in Experiments 1 and 2) because in those cases the mapping between 'seen direction' and 'felt direction' is more direct.

In summary, the current study suggests that simultaneous adaptation to retinal motion and pursuit does not produce MAE easily predicted on the basis of perceived motion. Our tentative conclusion is that this type of MAE is more likely to be based on the interaction between retinal and extra-retinal components.

There is one final feature of the data that is worth mentioning. A number of previous studies have shown retinal estimates of speed are larger than their pursuit-based counterpart (see Freeman et al. (2010), for review). This explains why the directions perceived in the R + P condition of Experiment 1 were skewed towards the object-dependent retinal motion. Curiously, the weight of evidence in the present experiments is that the speed of MAE following retinal adaptation is in fact *lower* than that produced by pursuit adaptation, despite the increase in perceived adaptation speed. Why this is the case remains to be determined.

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